A New Genus and Species of Neomphalid Limpet from the Mariana Vents with a Review of Current Understanding of Relationships among Neomphalacea and Peltospiracea

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ABSTRACT

Symmetromphalus regularis new genus, new species, is described from hydrothermal vents of the Mariana Back Arc Basin. It differs from *Neomphalus fretterae* McLean, 1981, in having the opening of the mantle cavity directed anteriorly rather than to the left, more numerous epipodial tentacles, the operculum retained in the adult, and in a deep sperm groove on the left cephalic tentacles of males.

The family Cyathermiidae is here proposed for two coiled members of the superfamily Neomphalacea, the genera *Cyathermia* and *Lacunoides*, both of Waren and Bouchet (1989). The family Cyathermiidae is characterized by: a short snout, a closed sperm groove along the left cephalic tentacle, and two cirri at the tip of the left cephalic tentacle.

Neomphalacea can be associated with Peltospiracea in a suborder Neomphalina, on the basis of shared characters (nonnacreous shell, monotocardian heart, bipectinate gill, lack of ctenidial bursicles, similar radula). As these may be plesiomorphic or convergent characters, further anatomical comparisons are needed to establish additional synapomorphic characters for such a suborder. A fossil record of the newly expanded complex is yet elusive, but should continue to be sought.

Key words: Archaeogastropoda; Neomphalacea; *Symmetromphalus*; Cyathermiidae; Peltospiracea; hydrothermal-vent limpets; Mariana Vents.

INTRODUCTION

Neomphalus fretterae McLean, 1981, the largest and most densely aggregated of hydrothermal-vent limpets, was the first vent-limpet to be described (McLean, 1981). Its anatomy was treated in an accompanying paper by Fretter *et al.* (1981). Although I expected that additional species of *Neomphalus* would eventually be found at other sites, none were found until the fauna of the Mariana Back Arc Basin was sampled in 1987, at which time a new, monotypic genus in the family Neomphalidae was discovered. The primary objective of this paper is to provide the formal description of the new genus and species *Symmetromphalus regularis*.

Recently, an affinity with *Neomphalus* was recognized in two coiled genera described by Waren and Bouchet (1989) from Eastern Pacific hydrothermal vents: *Cyathermia* and *Lacunoides*. These small-shelled, monotypic genera are regularly coiled and have many of the diagnostic features common to *Neomphalus*, although they share other unique features, which indicate that they in turn should be segregated within their own family. Accordingly, the family Cyathermiidae is here proposed.

Higher classification of Neomphalacea and the recently proposed and probably related Peltospiracea McLean (1989a) has been discussed by Haszprunar (1988a,b, 1989), Waren and Bouchet (1989), and Fretter (1989). Another objective of this paper is to briefly review the current work that assesses these relationships, noting the gaps in our understanding of anatomy in certain members.

My early interpretation of the possible fossil affinity of *Neomphalus* has generated some controversy; here I take the opportunity to review these criticisms and offer a revised assessment of the potential for a fossil record of the groups treated here.

MATERIALS AND METHODS

The new species described here was first collected with the deep-submersible *Alvin* in May, 1987, at hydrothermal vents of the mid-Pacific Mariana Back Arc Basin. A general description of the site was given by Hessler *et al.* (1988). Until now, two other gastropods, *Alvinoconcha hessleri* Okutani and Ohta, 1988, and *Pseudorimula marianae* McLean, 1989b, have been described from these vents.

Limpet specimens were collected with the mechanical arm of the *Alvin* in the course of collecting substrate samples and general collecting of all organisms. Material was preserved upon reaching the surface and was originally fixed for 24 hours in 10% seawater formalin buffered with sodium borate, washed in fresh water, and transferred to 70% ethanol (for details of collecting pro-

cedures see Turner *et al.*, 1985). Preserved specimens were sorted at Scripps Institution of Oceanography and forwarded to me by Robert R. Hessler.

Radulae were extracted from preserved specimens after dissolution of tissues with 10% NaOH for 48 hours, air dried and coated with gold palladium for SEM examination. Juvenile shells with protoconchs were examined with SEM. Protoconch lengths were taken directly from scale indications for the SEM micrographs.

Repositories of the type material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum (USNM), and the Museum National d'Histoire Naturelle, Paris. All figured specimens are deposited at the LACM.

SYSTEMATICS

Superorder ARCHAEOGASTROPODA Thiele, 1925

Recent authors (Salvini-Plawen, 1980; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988a,b; Hickman, 1988) have discussed the problems inherent in the "archaeogastropod" concept, pointing out that Archaeogastropoda, as traditionally constituted (Thiele, 1925; Knight *et al.*, 1960) represents a grade.

Hickman (1988) redefined Archaeogastropoda to include superfamilies Pleurotomariacea, Fissurellacea, and Trochacea, stating that it was thereby synonymous with Haszprunar's concept of Vetigastropoda Salvini-Plawen, 1980. However, Haszprunar (1988a,b) also included Lepetodrilacea McLean, 1988, in Vetigastropoda, which inclusion was overlooked by Hickman (1988) and also by Bieler (1990:380) in his critique of Haszprunar's work. I follow Haszprunar (1988a,b) in retaining the traditional meaning of Archaeogastropoda, allowing it to be expressly indicated in a classification as an orthophyletic grade.

Superfamily NEOMPHALACEA McLean, 1981

The diagnosis that follows encompasses two families, the Neomphalidae and the Cyathermiidae new family, taking into account the characters of the two coiled genera described by Waren and Bouchet (1989). It will, however, need to be modified once the internal anatomy of all genera becomes known.

Diagnosis: Shell regularly coiled or of limpet form, lacking nacre periostracum thick; first teleoconch whorl with oblique aperture and rounded whorls, regularly coiled in all genera, protoconch with net-pattern surface sculpture; operculum multispiral initially, final volution enlarged, retained at least through the first teleoconch whorl in all members

Monotocardian, ventricle not penetrated by rectum; left kidney only, ctenidium bipectinate, afferent membrane lacking or very short gill axis producing sturdy free tip, filaments elongate skeleton lacking bursicles. Perioral surface with transverse furrow extending to ce-

phalic lappets. Eyes lacking, epipodial and cephalic tentacles non-papillate, left cephalic tentacle of male modified to function as penis, sperm groove open or closed. Gonad with glandular gonoducts, dorsal to digestive gland and intestine; females with seminal vesicle.

Radula rhipidoglossate, cusps of all teeth aligned in descending rows, shaft lengths of all teeth increasing toward edge of ribbon. Rachidian tooth with shaft broad at base and acutely pointed overhanging cusp. Lateral teeth four pairs, inner surfaces excavated to articulate with rachidian or adjacent lateral teeth, overhanging cusps of laterals like those of rachidian tooth. Marginal teeth numerous, shafts wide but incompletely separated at base, tips deeply serrate.

CYATHERMIIDAE new family

Diagnosis: Shell coiled through teleoconch; sculpture smooth to finely reticulate. Neck short; short snout present; cephalic tentacles anterio-laterally directed; enlarged left tentacle serving as penis, sperm groove of enlarged left tentacle closed, tip with two prominent cirri. Afferent ctenidial membrane very short. Cusps of rachidian and lateral teeth finely serrate, cusp of rachidian tooth much longer than those of inner lateral teeth.

Included genera: *Cyathermia* Waren and Bouchet, 1989, and *Lacunoides* Waren and Bouchet, 1989. *Cyathermia* is monotypic for *C. naticoides* Waren and Bouchet, which is widely distributed on the East Pacific Rise. *Lacunoides* is monotypic for *L. exquisitus* Waren and Bouchet, known only from the Galapagos Rift.

Remarks: Separation of the two monotypic coiled genera from the two monotypic limpet genera is now appropriate at the familial level, given that each of the two groups of genera have synapomorphic characters in common. Diagnostic characters of the Cyathermiidae are the short snout, left cephalic tentacle with closed sperm groove and two cirri at the tip, serration of rachidian and lateral teeth and enlargement of rachidian tooth. See Waren and Bouchet (1989) for more detailed descriptions of these two genera.

Family NEOMPHALIDAE McLean, 1981

Diagnosis: Shell coiled through first teleoconch whorl, changing to limpet form in second teleoconch whorl; sculpture of strong radial ribs. Neck long; snout lacking in adult; cephalic tentacles posteriorly directed; sperm groove of enlarged left tentacle open; cirri at tip of penis lacking. Cusps of rachidian and lateral teeth non-serrate, cusp of rachidian tooth of same length as those of inner lateral teeth.

Included genera: *Neomphalus* McLean, 1981, and *Symmetromphalus* new genus. *Neomphalus* is monotypic for *N. fretterae* McLean, 1981, known from the Galapagos Rift (the type locality) and from sites on the East Pacific Rise. *Symmetromphalus* is monotypic for *S.*

regularis new species, known only from the Mariana Back Arc Basin vents.

Remarks: Diagnostic characters of the Neomphalidae are the limpet form of the mature shell, absence of snout, posterior direction of cephalic tentacles, open sperm groove and lack of cirri on the enlarged left tentacle. See Fretter *et al.* (1981) for a more detailed description of anatomy in *Neomphalus fretterae*.

Symmetromphalus new genus

Type species: *Symmetromphalus regularis* new species.

Description: Shell of limpet form, mantle cavity and horseshoe-shaped muscle open anteriorly; shell outline symmetrical in juvenile, irregular in mature specimens; coiled apical whorl offset to right. Sculpture of finely beaded radial ribs; operculum present in adult. Neck long, perioral surface with transverse furrows extending to cephalic lappets. Cephalic tentacles short, posteriorly directed, left tentacle of male greatly distended, deep dorsal sperm groove connecting with groove on left side of neck. Epipodial tentacles present posteriorly and laterally. Gill bipectinate, afferent membrane lacking, filaments elongate, efferent axis of free tip extended over long neck. Radula rhipidoglossate, four pairs of lateral teeth, cusps similar to those of rachidian teeth, except fourth lateral teeth strongly serrate on outer edge; marginal teeth numerous.

Remarks: On characters of external anatomy, *Symmetromphalus* differs from *Neomphalus* in its: anterior rather than leftward opening of the mantle cavity and shell muscle, its evenly distributed rather than posteriorly grouped epipodial tentacles, smaller cephalic tentacles, greater prominence of sperm groove in enlarged left cephalic tentacle, and apparent absence of well-defined food groove. The shell differs in having strong beading on early ribs and lacking the interior ridge. A vestigial operculum is present in mature specimens. The radula is similar in both genera.

Most of these distinctions are regarded as significant at the generic level. Only the sculptural difference (prominent beading rather than smooth ribs) is considered a species-level difference by itself.

Names of both the new genus and species emphasize the regular and symmetrical aspect, in contrast to the leftward shift of the mantle cavity that characterizes *Neomphalus*.

Symmetromphalus regularis new species

(figures 1–17)

Description: Shell (figures 1–3, 7–10, 17) of medium size for family (maximum length 14.0 mm for females, 10.6 mm for males), white under thick, pale tan periostracum, which projects beyond edge of shell. Profile moderately elevated; juvenile shell nearly symmetrical, outline of mature shell irregular, indicating habitual site of

attachment. Apical whorl markedly posterior in juvenile shell (figures 11, 12), closer to center in mature shell. Protoconch (figures 13, 14) length 220 μm, surface sculpture of irregular network of low ridges. First teleoconch whorl rounded, suture deep, coiled through one-half whorl of growth. Limpet form attained after completion of first teleoconch whorl; growth of posterior slope beginning at shell length of 1.5 mm. Radial (spiral) sculpture arising at shell length of 1 mm, consisting of low primary cords on which beading appears at shell length of 2 mm. Secondary cords arise at shell length of about 7 mm, quickly assuming size of primary cords; cords at margin very narrow, retaining beading, interspaces broad. Shell interior glossy white. Muscle scar horseshoe-shaped, open anteriorly, broad throughout, except posteriorly; anterior terminations rounded. Apical pit remaining open.

Dimension of holotype (female): Length 12.3, width 10.1, height 5.0 mm; dimensions of illustrated paratype (male): length 8.4, width 6.5, height 3.0 mm.

External anatomy (figures 4–7, 9): Neck long, wide, dorso-ventrally compressed, lateral edges acutely angulate (except left edge deeply grooved in male). Transverse furrow extending laterally above mouth, delimiting the ventrally positioned oral lappets. Eyes lacking, cephalic tentacles posteriorly directed, equal and relatively short and thin in females (contracted state); left tentacle of male enormously distended, bearing a deep sperm groove dorsally, which is continuous with deep groove on left edge of neck. Females lack groove on left edge of neck.

Mantle cavity deep, extending two-thirds the length of shell muscle on left side. Ctenidium bipectinate, afferent membrane lacking throughout its length, efferent axis arising at posterior of mantle cavity on left; free tip of gill separating above base of neck, its efferent axis massive, extending well anterior of head; gill filaments overlying head, greatly elongate, decreasing in length toward tip.

Mantle margin with fine papillae corresponding to radial ribs. Outline of foot rounded; anterior edge of foot with furrow marking opening of pedal gland. Epipodial ridge encircling foot, extending forward on both sides to join with neck edges; short, contracted epipodial tentacles evenly spaced along ridge, becoming smaller anteriorly, not extending anteriorly beyond position of shell muscle. Operculum (figure 9) very thin, transparent, multispiral, with rapidly enlarging final whorl, edge frayed, shed in some large females (largest operculum about 4 mm diameter).

In dorsal view of detached animal, shell muscle arms very broad, except posteriorly, where reaching one-fifth the maximum width; anterior terminations rounded, mantle skirt thin, showing posteriormost extent and outline of ctenidium; pericardium visible as dark structure posterior to gill; gonad and pallial gonoducts large, overlying digestive gland, occupying posterior dorsal area next to right arm of shell muscle (figure 4).

Radula (figures 15, 16) rhipidoglossate, rachidian and

Figures 1–10. *Symmetromphalus regularis* new species, from Alice Springs vents, Mariana Back Arc Basin, *Alvin* dive 1843, 3,640 m. Anterior at top in dorsal and ventral views. **1–6.** Holotype (female), LACM 2432, shell length 12.3 mm. **1.** Shell exterior. **2.** Shell interior. **3.** Left side of shell. **4.** Dorsal view of detached body. **5.** Ventral view of detached body. **6.** Left lateral view of detached body. **7–10.** Paratype (male), LACM 2433, shell length 8.4 mm. **7.** Dorsal view of detached body. **8.** Shell exterior. **9.** Ventral view, animal attached to shell, showing operculum on edge. **10.** Left side of shell.

four pairs of lateral teeth of similar morphology, marginal teeth numerous; cusp rows of all teeth forming circular arc. Base of rachidian teeth broad, overhanging cusp moderately long, tapered to acute tip. First lateral tooth slightly less prominent than rachidian tooth, inner base behind that of rachidian tooth. Second, third and fourth lateral teeth similar to each other, their innermost bases behind the base of adjacent lateral teeth; lengths
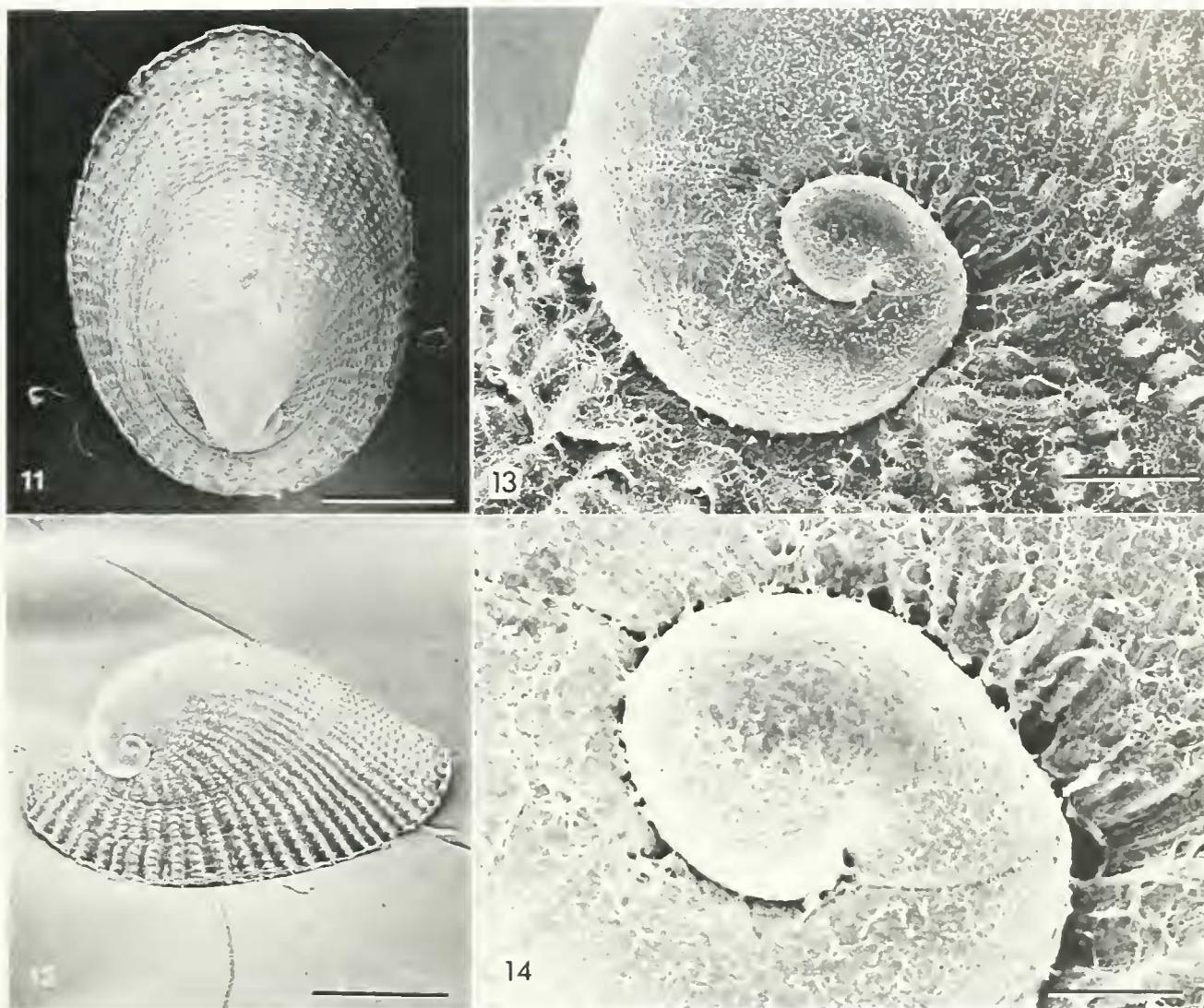
Figures 11–14. *Symmetromphalus regularis* new species. SEM views of juvenile paratype, LACM 2433, shell length 3.5 mm. 11. Dorsal view. 12. Oblique, left lateral view. 13. Protoconch and early sculpture, scale bar = 200 μm 14. Protoconch, scale bar = 100 μm

of shafts and overhanging cusps increasing in length outwardly. Fourth lateral tooth larger than third, its outer edge sharply serrate, its lowermost serration most prominent. Inner marginal teeth with long, broad shafts, cusp edges deeply serrate; shafts of outer marginal teeth incompletely separated.

Type locality: Alice Springs vents, Mariana Back-Arc Basin (18°12.6'N, 144°42.4'E), 3,640 m. The limpets occur in dense aggregations on the walls of the vents (figure 17). From the photograph it is evident that the limpets are oriented randomly, filling all space on the substrate, but not stacked.

Type material: 27 specimens from type locality, *Alvin* dive 1843, 4 May 1987. Holotype LACM 2432, 10 paratypes LACM 2433, 10 paratypes USNM 784763, 6 paratypes MNHN. All specimens have undamaged perios-

traca, free of biogenic or mineral encrustations. Males are represented by six specimens only, of which the smallest (with broken shell) is approximately 5 mm in length. Twelve specimens under 5 mm in length are too small to sex without sectioning.

DISCUSSION

Higher Classification

The affinities and the higher classification of the Neomphalacea are yet to be fully resolved and are likely to remain controversial for some time. Fretter *et al.* (1981) affirmed that *Neomphalus* is a highly derived archaeogastropod, but could not relate it to other known living groups. Waren and Bouchet (1989) placed the newly described family Peltospiridae McLean, 1989, in the
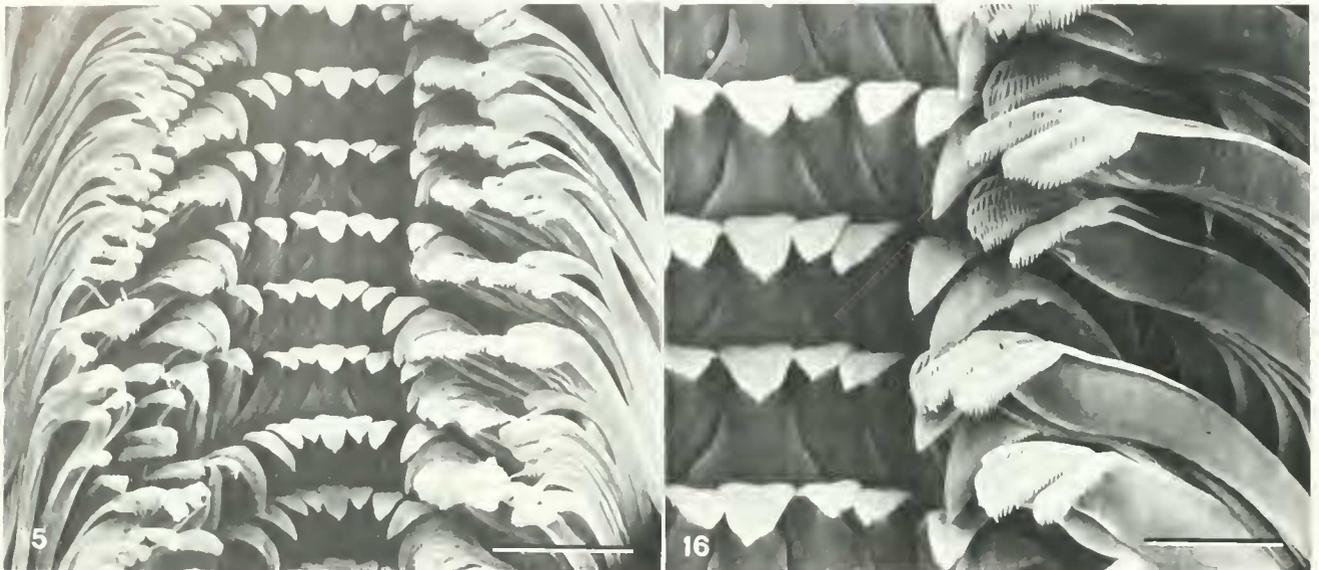
Figures 15, 16. *Symmetromphalus regularis* new species. SEM views of radula of paratype. 15. Full width of ribbon, showing rachidian, four pairs of lateral teeth and numerous marginal teeth, scale bar = 40 μm. 16. Enlarged view of overhanging cusps of rachidian, laterals and marginals, scale bar = 20 μm.

Neomphalacea, whereas McLean (1989a), Fretter (1989), and Haszprunar (1988a,b, as hot-vent group A) separated two superfamilies: Neomphalacea and Peltospiracea. Shared characters of both superfamilies include the monotocardian heart, bipectinate ctenidia that lack bursicles, oesophageal features, statocysts with statoliths, and radular similarity. In having the left kidney only and in lacking ctenidial bursicles both groups were placed outside the Vetigastropoda (superfamilies Scissurellacea, Pleurotomariacea, Fissurellacea, Haliotacea, Trochacea,

and Lepetodrilacea) by Salvini-Plawen and Haszprunar (1987) and by Haszprunar (1988a,b). Both groups were regarded as generally more primitive than the Vetigastropoda by Haszprunar.

The main argument for separation of Neomphalacea and Peltospiracea concerns the striking differences in external features that are related to feeding modes: in Neomphalacea the neck is long and dorso-ventrally compressed; transverse furrows lead from the recessed mouth to protruding lappets that are ventral to the cephalic

Figure 17. *Symmetromphalus regularis* new species. In situ view of limpets on basalt boulders in path of effluent at Alice Springs, Mariana Back Arc Basin, 3,640 m. The largest limpets may exceed 14 mm in length. Photo courtesy S. Ohta.

tentacles (see Waren & Bouchet, 1989. fig. 23 for *Cyathermia*), and there is a notch for dorsal access to the mouth from the food groove (well-developed only in *Neomphalus*), the bipectinate gill is hypertrophied, the gill filaments elongate and separated for filter feeding in combination with grazing. In contrast, the Peltospiracea are known by the descriptive appellation of 'tapersnouts,' which was first used by McLean (1985) prior to their formal description, because of their long, tapered snouts. The tapered snout was correlated by Fretter (1989) with a well-developed, protrusible subradular organ, enabling the snout to project at great length.

The Peltospiridae include both limpet-shaped and coiled members. Two important papers on anatomy of peltospirids have been published, that of Fretter (1989) on anatomy of the limpets and the subsequent paper of Haszprunar (1989) on the anatomy of the coiled *Melanodrymia*. Unfortunately Haszprunar did not have benefit of access to the manuscript of Fretter (1989), so that comparisons could not be made. *Melanodrymia* is atypical of peltospirids in several respects: having both the left and right tentacles modified for copulation (unlike the peltospirid limpets or other coiled peltospirids), and lacking skeletal rods in the ctenidium. It may be that *Melanodrymia* is not a true peltospirid, although Haszprunar elected not to establish a family for it.

Anatomical comparisons between all supposed peltospirids are needed. The limpet *Hirtopelta* McLean, 1989a, lacks a tapered snout and represents a genus not strictly peltospirid. Another unresolved problem has been noted: there are two different protoconch types (net sculpture and longitudinally ribbed) both in limpet genera and coiled genera (McLean, 1989a; Waren & Bouchet, 1989).

Knowledge of the internal anatomy of *Cyathermia* is also needed. Because it is regularly coiled, it seems evident that *Cyathermia* is less derived and probably a better representation of neomphalacean anatomy than *Neomphalus*, although the Cyathermiidae seem to have more complex reproductive modifications in having cirri at the tip of the copulatory appendage. *Symmetromphalus*, the new genus described here, is less derived than *Neomphalus*, for the reason that its symmetry is typical of all other prosobranch limpets, its torsion not carried through an additional 90 to place its mantle cavity on the left, as in *Neomphalus*. *Neomphalus* is also more derived in having a well-defined food groove and a gill that is larger and thereby more effective than that of *Symmetromphalus*.

Radular similarities between Neomphalacea and Peltospiracea need not indicate close affinity. Hickman (1983) first discussed both radular types, and in 1984 reported that the radula of *Melanodrymia* was similar to that of *Neomphalus* and that both could represent an "unspecialized grade of rhipidoglossate radular evolution." Haszprunar (1989) agreed that radular similarities could be "plesiomorphic and should not be overemphasized in tracing phylogenetic relationships." A similar case of radular uniformity is known in the earliest ontogenetic stages of most trochaceans (Waren, 1990).

One can unite the superfamilies Neomphalacea and Peltospiracea within a suborder Neomphalina based on such shared characters as the similarity of the unspecialized radulae, lack of nacre, and lack of ctenidial bursicles, but these are plesiomorphic, grade defining characters. It is difficult to identify apomorphic characters to define such a suborder. We are left with negative characters that suffice to remove both superfamilies from other well-defined suborders. In spite of the present difficulties in justifying a suborder Neomphalina within a rigorous cladistic framework, I expect that the original hypothesis of Waren and Bouchet (common ancestry for Neomphalidae and Peltospiridae) will eventually be accepted.

An alternative view of the affinity of *Neomphalus* was given by Sitnikova and Starobogatov (1983), in a short, unillustrated paper in which they placed *Neomphalus* in their new suborder "Neomphaloidei" [sic] in the order Vivipariformes Sitnikova and Starobogatov, 1982. A translation of the original Russian has been obtained, courtesy David R. Lindberg. The radula of *Neomphalus* was said to lack a lateromarginal plate and to have marginal teeth that are not distributed in groups of small secondary teeth as in rhipidoglossate radulae of trochid, turbinid, and neritid species. Marginal teeth of *Neomphalus* were said to be more similar to the marginal teeth in the architaenioglossate radula, particularly the genus *Leonia* in Pomatiidae, despite the fact that there are only two pairs of marginal teeth in *Leonia*. Other shared characters cited were elongate mantle cavities and looped pallial gonoducts.

Waren and Bouchet (1989) dismissed the Sitnikova and Starobogatov phylogeny of *Neomphalus* as not to be taken seriously in the absence of detailed evidence, and objected to the placement of *Neomphalus* among the Mesogastropoda. I agree that a more convincing exposition of the theory needs to be presented. The radular argument seems irrelevant to me: why should the neomphalacean radula be structured like that of other known rhipidoglossate groups? Nothing is said to falsify the interpretation that it is a relatively unspecialized rhipidoglossate radula. Recently, Golikov and Starobogatov (1988) introduced 36 new prosobranch suborders while maintaining the order Vivipariformes with suborders Neomphaloidei, Viviparoidei, and Valvatoidei. This was done without knowledge of the later introduction of Peltospiracea (McLean, 1989a; Waren & Bouchet, 1989, Fretter, 1989) and of recent work on Valvatidae (Rath, 1988), which resulted in the placement of Valvatacea in the subclass Heterobranchia by Ponder and Waren (1988).

An article in Japanese entitled "New archaeogastropod superfamily Neomphalacea" by Nakamura (1986) is not to be taken as a proposal of a homonym for the superfamily; rather it is evidently a review note intended for Japanese readers.

FEEDING BIOLOGY

Haszprunar (1988b) suggested that "*Neomphalus* itself probably does not feed by filter-feeding alone, but pos-

sibly by symbiotic chemoautotrophic bacteria and/or by grazing bacterial films like some other molluscs of the hydrothermal vents. This is indicated by its radula, which is not like those of typical filter feeders. . . ." Original reports on *Neomphalus* of McLean (1981) and Fretter *et al.* (1981) made it clear that part of its nutrition is derived from grazing, particularly in the younger stages. Symbiotic chemoautotrophic bacteria are associated with most bivalves in the hydrothermal-vent community, but the only vent-associated gastropod for which this relationship is known is *Alvinoconcha hessleri*, as reported by Stein *et al.* (1988). Stein (personal communication) has informed me that other vent limpets have been subjected to biochemical assay (ribulose-1,5-diphosphate carboxylase) for chemoautotrophic symbionts, but the negative results were not published. There is, however, a report by de Burgh and Singla (1984) of bacterial colonization of the gill surface and direct endocytosis of the bacteria in the limpet subsequently described as *Lepetodrilus fucensis* McLean, 1988.

Haszprunar's comment that the radula of *Neomphalus* is not like that of typical filter-feeders is not relevant, because the radulae of filter feeding gastropods in such superfamilies as Trochacea, Cerithiacea, and Calyptraeacea are subject to the phylogenetic constraints of the radular plans typical of each group. A typical filter-feeding radula can therefore not be defined. The radula of a filter-feeding gastropod functions primarily to rake in a food string, for which many possible morphologies are suitable.

FOSSIL RECORD

A direct fossil record for any neomphalacean or peltospiricean shell morphology remains to be established. In my earlier assessment of *Neomphalus* (McLean, 1981), I suggested that there may be a link between Neomphalacea and the Paleozoic Euomphalacea, which I had (somewhat rashly) emphasized by placing both in a therein proposed suborder Euomphalina. The thrust of my argument was as follows: given that euomphalaceans have been regarded as immobile and therefore potential filter-feeders (references in McLean, 1981), a gill like that of Neomphalacea could have provided the mechanism by which filter-feeding was possible in Paleozoic euomphalaceans.

Although most subsequent authors have ignored my functional argument, Runnegar (1983) took notice of it. He did "not wish to disagree with any of this," but had difficulty with the resulting classification. Batten (1984) found no similarities in shell structure between Neomphalacea and Paleozoic Euomphalacea. Bandel (1988) removed from Euomphalacea all Mesozoic genera mentioned by McLean (1981) as possible links between the two groups. While the latter two authors have found no ... supporting the connection, it can still be argued ... tion to Paleozoic euomphalaceans (or pos... ... through unknown intermediate steps ... Now that *Cyathermia*, as well as the

entire peltospiracean complex, is known, it may be easier to conceive of a connection leading to other living genera.

Sitnikova and Starobogatov (1983) stated that a connection between *Neomphalus* and euomphalaceans was falsified because Euomphalacea had paired gills (on the basis of the spiral keel in some euomphalacean genera), but that rather dogmatic assumption is not generally accepted and to me seems poorly founded and unlikely. The shell of *Cyathermia* has a deep sinus in the outer lip (see Waren & Bouchet, 1989: figs. 6, 7), which is undoubtedly related to projection of the single bipectinate gill. This evidence suggests to me that a hypertrophied single gill like that of Neomphalacea would better correlate with spiral keels or sinuses in the lips of euomphalaceans (see McLean, 1981: fig. 13) than would paired gills.

The coiled genera *Cyathermia* and *Lacunoides* demonstrate that the typical neomphalacean gill and mouth with dorsal access to ctenidial filaments can function in mature, coiled snails. These coiled snails are mobile, but they are also smaller, of a size comparable to the juveniles of *Neomphalus* and *Symmetromphalus*. We have yet to discover a larger, coiled member of the Neomphalacea, but there is no reason to assume that it could not function as a sedimentary filter feeder. However, we are not likely to find such a member of Neomphalacea in the hydrothermal-vent habitat, as it would be more prone to shell crushing by the brachyuran predators in the hydrothermal environment.

Now that we have recognized major radiations comprising the superfamilies Neomphalacea and Peltospiracea, as well as the Lepetodrilacea (see McLean, 1988; Fretter, 1988), which superfamily is not discussed here, I continue to believe it likely that these groups must have had a fossil record in the Paleozoic and early Mesozoic, the time at which all living archaeogastropod superfamilies diverged (more detailed discussion in McLean, 1981, 1985, 1988, 1989a,b). There are numerous extinct gastropod clades of the Paleozoic and Mesozoic, which are assumed to have been rhipidoglossate archaeogastropods, for which the anatomical plan remains conjectural (see Knight *et al.*, 1960). The enormously plastic Peltospiracea and the newly expanded Neomphalacea have only been introduced into the literature for slightly over one year, hardly enough time for paleontologists with interests in Paleozoic and Mesozoic faunas to have searched for connecting links.

BIOGEOGRAPHIC IMPLICATIONS

The Mariana Back Arc Basin vents are isolated from all other known hydrothermal sites, yet they contain some faunal elements in common with those of other sites, in addition to faunal elements found nowhere else. Only one mollusk, the lepetodrilacean limpet *Lepetodrilus elevatus* McLean, 1988, occurs widely at vents on the Galapagos Rift and at all hydrothermal vent-fields on the East Pacific Rise as well as at the Mariana vents (McLean, unpublished). There is also a faunal connection of the

Mariana vents to the vents of the Mid-Atlantic Ridge; *Pseudorimula* McLean, 1989, has an undescribed congener at the Mid-Atlantic Ridge (McLean, in preparation). Hessler *et al.* (1988) suggested that hydrothermal vents associated with past spreading centers are likely to account for these widely disjunct distributions. Tunnicliffe (1989) discussed the vicariant events that shaped the present distributions of hydrothermal-vent faunas shared by the East Pacific Rise and the Juan de Fuca/Gorda Ridge systems. The vicariant events that would allow interchange between the eastern Pacific ridge systems and the Mariana Back Arc Basin remain to be treated in the literature. Vast amounts of geologic time must surely be involved, in view of the slow, step-by-step dispersal of vent archaeogastropods that is necessitated by their lack of planktotrophic dispersal stages (for review see Lutz, 1988).

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